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THE PROBABLE INFLUENCE OF DISTURBED NUTRITION ON THE EVOLUTION OF THE VEGETATIVE PHASE OF THE SPOROPHYTE.

BY GEO. F. ATKINSON.[1]

In this paper the discussion of the influence of nutrition, applies chiefly to that source of nutrition in plant organs provided with chlorophyll, and presupposes, in general, that the ordinary physiological processes, other than the one which is termed carbon assimilation, are normal. In all such plants some development of this vegetative part of the plant must take place before spore production, or fruiting, of a kind which represents a real increase at the time, can be accomplished. Some apparent, but not real, exceptions to this might be noted. In germination of the spores of Oedogonium, frequently spore production takes place without the development of any such vegetative part of the plant, but there is no real increase of the plant substance. This kind of spore production is only a means, perhaps, to tide over some condition unfavorable for the elaboration of the vegetative phase of the plant, which is present at the time and place. In Coleochæte, germination of the oospore results in the formation of a cellular mass, which is larger than the oospore, breaks the enclosing wall, and the cells escape as a number of zoospores in place of one. But in this oospore are the stored products of carbon assimilation of the parent chlorophyll phase of the plant, and this case only differs from that of the Bryophyta, in that the sporophyte becomes separated, with stored products, from the gametophyte, before the differentiation of the spores.

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[1] Cornell University.

In the higher plants many cases of bulbs, corms, tubers, etc., might be cited to show that the development of the sporophylls, and even fruit, might take place without the accompaniment of chylorophyll bearing organs. But here also the bulbs, corms, etc., represent, in the stored products of carbon assimilation, the preceeding green leaves. In certain ferns, as Osmunda cinnamomea, the sporophyll, which is completely differentiated from the vegetative leaf, appears first in the spring, and could mature its spores without the aid of the vegetative leaves of that season, but the green leaves of the previous season formed the necessary carbohydrates, which are stored in the rhizome and rudimentary leaves during the winter and in fact the sporophylls and sporangia are partly developed at the close of the previous season.

We might say, then, that in general, all spore production in plants, which themselves assimilate carbon dioxide, is necessarily preceeded by a greater or lesser development of chlorophyll bearing organs. This may appear to be a too well known axiom for even the brief discussion here given, but it is necessary in view of what is to come to have this axiom well in mind. Chlorophyll bearing organs, or tissues, then, as compared with sporogenous organs or tissues, are, in point of time within the life cyle, *primary,* while the latter are *secondary.* This proposition should not be regarded as opposed to the primary evolution of the sporophylls as compared with the foliar organs of the sporophyte. It applies only to a comparatively limited extent of time; to the usual cycle between the vegetative and fruiting phases; to the ontogenetic, not to the phylogenetic, development. It applies with equal force to plants in which either the gametophyte or the sporophyte forms the chlorophyll bearing organ.

There is a strong tendency in nature to an economy in the distribution of the food supply between foliar, and sporophyllary, organs; between the vegetative and fruit products of the plant. This is well seen in the varying sizes of plants having varying amounts of food supply, where with limited food supply small plants have few and small leaves accompanied by a limited out-put of fruit (other conditions are considered normal); while with increasing amounts of food, other things being equal, each of these plant products is increased, though not in the same ratio. With high feeding the vegetative increase shows a higher ratio than the fruiting. The food may be so abnormally abundant as to cause an abnormally abundant vegetative growth, accompanied in some cases with rudimentary fruit, or in others with the entire suppression of the fruit. In some rare cases it may be accompanied by the transformation of the sporophyllary organs to vegetative ones.

These facts teach that the fruit product, or sporophyllary development of plants is very sensitive to food supply, requiring a certain amount of food for perfection in even small quantities, increasing with additional food supply up to a given point, when it decreases again to zero; or in rare cases the sporophyllary organ may be transformed to a vegetative one, so antagonistic has the ratio between the vegetative and sporophyllary organs become because of the abnormally favorable conditions for vegetative growth. In addition to the sensitiveness which the fruit organs exhibit to varying amounts of food derived from the soil, they are very sensitive to disturbances in the supply of carbohydrates as a result of carbon assimilation in the vegetative organs, especially of a kind which partly or completely cuts off that supply. This is well seen in the diminished crops as a result of injury to the leaves at critical periods from insects or fungi, or as result of unfavorable meteorological conditions.

When the nutritive supply of the carbohydrates is suddenly disturbed by certain kinds and amounts of injury to the foliage leaves, or by pruning severely, thus cutting off a large number of forming or developed leaves, certain parts of the plant, either simple or in a rudimentary condition of development, have the function of carbon assimilation forced upon them to save the plant from destruction and to provide for the development of the fruiting organs. As is well known, latent buds, which have been in a dormant condition, may be, for years, are frequently in such cases stimulated to development and form leafy shoots. It is a very common occurrence as a result of severe pruning or of injury to the ordinary leaves for young flower axes, or buds, to develop leafy shoots with other flower buds in the new leaf axils. There is a tendency here to force the vegetative function upon the young flower axes, and if this influence is felt before the specialized character of the floral organs has been developed from the cells at the apex of the axis, the development of these organs will be deferred, while these cells assume the form and function of vegetative organs. This is a matter, perhaps, of common observation as a result of severe pruning, and in some plants can be very easily demonstrated by trial. But it serves well to show the influence of disturbed nutrition on other or dormant parts of the plant when the function of the existing vegetative leaves is arrested. That function is forced from the ordinary and well developed organs upon undeveloped or rudimentary ones, which readily under this influence adapt themselves to continue this important office. This must not be regarded as an attempt to explain the development of adventitious or supernumerary buds, etc., or latent buds, in all cases, into leaf branches. Local stimuli, and a number of other causes at times, call forth leafy shoots from these. Nevertheless, in view of what has been said above, the following proposition might be formulated. Nutrition disturbed, and the development of the fruit product of the plant being threatened, by the loss of carbon-assimilating organs, the function of the latter may be taken up by some other part of the plant, either rudimentary or undifferentiated, their development into said organs being a direct result of that disturbance.

In the cases dealt with above, the function is either transferred to latent vegetative organs, or to undifferentiated tissues. It is, therefore, simply and easily comprehended. Observations have been made, however, which tend to show that in the Angiosperms the vegetative function can be assumed not only by the floral envelopes, but also by the sporophyllary organs, more commonly by the macrosporophylls, or gynæcium. In some cases these open and expand into green leaves with the ovules, in a more or less imperfect stage of development, exposed. Perhaps no definite experiments have been carried out to demonstrate the cause of this transformation of form and function. It is supposed to be due to either excessive nutrition, or to some injury to the vegetative system of the plant. While such cases are unsatisfactory because of the lack of definite tests, they indicate that the sporophylls can assume the form and function of foliar organs when there is a disturbance of nutrition of a kind considered above. Since these sporophylls are, from a morphological standpoint, considered homologous with the green leaves, this change of function is not incompatible with that theory.

In the Pteridophytes direct experimentation proves beyond a doubt, that the sporophylls can be made to assume the form and function of the foliar organs by cutting off the latter, thus disturbing the nutrition and forcing the vegetation function on the sporophylls. The experiments performed upon *Onoclea sensibilis* and *O. struthiopteris* may be cited. In these cases after cutting off the early developed vegetative leaves the sporophylls appeared later in all stages of transformation, some complete vegetative leaves with only vestigial remnants in the form of rudimentary indusia to indicate to which series of organs they primarily belonged in the ontogeny of the plant. Between these and perfect sporophylls all gradations of intermediate forms occurred, the terminal portions of the sporophyll and of the pinnæ always being more fully expanded, while the basal portions of the same partook more or less completely of the true sporophyll. The details of the experiment and of the gradations of the development are given elsewhere, and cannot be dwelt upon here.

As an outgrowth of these experiments and observations a second proposition may be formulated as follows. Disturbed nutrition, resulting from the loss of the carbon assimilating organs of the sporophyte (vegetative leaves), may, and does, force the vegetative function on the sporophylls, causing them to develop into more or less complete vegetative leaves.

The experiments on Onoclea convince me that there are a number of Pteridophytes, as well as Phanerogams, which would yield the same results following the amputation of their leaves, when carefully conducted, especially in those plants where, during one season, the vegetative leaves are developed sometime in advance of the sporophylls. Plants like some of the Lycopods would make extremely interesting ones to work with, and especially in the case of some of these should I expect to see a transformation of the sporophylls into vegetative leaves. This would be entirely in harmony with the relation and development of these organs. In species of Lycopodium and Selaginella all gradations between sporophylls with normal sporangia and the vegetative leaves can be found. The transitional stages are marked by the gradual degeneration of the sporangia on some of the leaves, the sporophyllary character being shown only by vestiges of the sporangia. Bower has shown how the strobilus of the Lycopods elongating by apical growth would result in the increase in the number of the sporophylls, and that the demand thus made on the vegetative system for nutrition would result in the transformation of some of the sporophylls to foliage leaves, accompanied by a corresponding sterilization of some of the sporangia. Practically it would disturb the balance of nutrition between the sporophyllary and vegetative systems, the effect being the same as it would be if some of the foliage leaves were destroyed.

In view of the ultimate purpose of this paper the question must be raised here as to whether this transformation of the sporophylls to foliar organs is a case of reversion, or whether it is an advance of a primary organ to a secondary organ of the sporophyte. It is my conviction that the latter alternative is the logical and true one, that we can by experimentation demonstrate phylogeny in ontogeny. Bower[2] has called attention to the importance which must be attached to the fact that the primary function of the sporophyte was not only the production of spores, but an increasing number; that the increase in the mass of sporongenous tissue was necessarily accompanied by a sterilization of potential portions of the mass for purposes of protection, support, and for the conduction of nutritive material. From this condition he reviews the theoretical grounds for the relegation of the spore-producing cells to a superficial position, and the eruption of outgrowths on which the sporangia are supported, citing as illustrations of the early conditions of these outgrowths the strobilus of Equisetum and Phylloglossum. From the latter he traces the development of the elongated and branched leafy stem of species of Lycopodium by continued apical growth of its strobilus, while the sporangia on some of the lower sporophylls would be arrested, and the sporophylls themselves would develop as foliage leaves. For these and similar reasons elaborated by himself, he concludes, rightly I think, that the sporophylls are, from a phylogenetic point of view, *primary*, while the foliage leaves are *secondary*.

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[2] Ann. Bot., VIII, pp. 345–365, 1894.

All the evidence which we have points to the fact that in the early development of the sporophyte, it was entirely dependent upon the gametophyte for nutrition including the supply of carbohydrates. The expanded green prothalloid structure performed the same function for the sporophyte, that foliage leaves of the sporophyte do in plants where this becomes independent of the gametophyte. This is practically true now in all the thalloid liverworts, and in all the Bryophyta is the sporophyte practically dependent upon the gametophyte for this function. In most of the Pteridophytes the sporophyte is dependent upon the gametophyte for its carbohydrates during the embryo stage. In some of the Pteridophytes, in the Gymnosperms, and in the Angiosperms, the gametophyte has entirely lost the function of carbon assimilation, this function being solely performed by parts of the sporophyte.

What influences led to the gradual transfer of this function of the gametophyte to parts of the sporophyte? Nutritive disturbances have been shown to play a very important part in the formation of sporophyllary organs quantitatively, in varying ratios between the vegetative and sporophyllary structures with increased food supply; in a tendency to produce a natural but variable equilibrium between these two functional kinds of organs; and especially in the transformation of sporophyllary organs to vegetative ones. If these disturbances, especially in the nature of partial or complete loss of carbon assimilating organs of the sporophyte produce such an effect, why should there not be a similar influence brought to bear on the sporophyte, when the same function resides solely in the gametophyte, and a disturbing element of this kind is introduced? To me there are convincing grounds for believing that this influence was a very potent, though not the only one in the early evolution of sporophytic assimilatory organs. By this I do not mean that in the Bryophyta, for example, injury to the gametophyte would now produce distinct vegetative organs on the sporophyte, which would tend to make it independent of the gametophyte. But that in the Bryophyte-like ancestors of the Pteridophytes an influence of this kind did actually take place appears to me reasonable.

In the gradual passage from an aquatic life, for which the gametophyte was better suited, to a terrestrial existence for for which it was unadapted, a disturbance of this function was introduced. This would not only assist in the sterilization of some of the sporogenous tissue, which was taking place, but there would also be a tendency to force this function upon some of the sterilized portions of the sporophyte, and to expand them into organs better adapted to this office. As eruptions in the mass of sporogenous tissue took place and sporophylls were evolved, this would be accompanied by the transferrence of the assimilatory function of the gametophyte to some of these sporophylls. Even the protophylls may have originated by the eruption of certain of the sterile portions of the sporophyte under the influence of disturbed nutrition.

The sporophyte from its nature presented greater possibilities in the way of the elaboration of a complex, robust, perennial inhabitant of terrestrial zones. Increased sporogenous tissue was necessarily accompanied with a more bulky structure, which then necessitated a differentiation of its tissue by sterilization of certain external, then internal, parts for protection and circulation. Robust types of land plants could more naturally be developed from such a phase than from the expanded and delicate gametophyte. When the sporophyte had largely assumed this function of the gametophyte, and by the development of absorbing organs in the soil was enabled to live an independent existence, it became gradually established, as conditions changed, in situations where the gametophyte could not exist. It has thus become the dominating vegetative feature of most land areas, while the gametophyte in these higher forms, has become an organ entirely dependent upon the sporophyte for nourishment, or has been developed into an organ to serve a secondary purpose in the nourishment of the sporophytic embryo.

PROGRESS IN AMERICAN ORNITHOLOGY.
1886–1895.

By R. W. Shufeldt, M. D.

What I have to say here in reference to the progress in American ornithology for the past nine or ten years is prompted by the recent appearance of the second edition of *The A. O. U. Check-List of North American Birds.* Most naturalists are familiar with the first edition of this work, it having been published in 1886. It was officially promulgated by the American Ornithologists' Union, and zoologists the world over have carefully considered " The Code of Nomenclature " that formed a part of the volume. Moreover, it contained a List of North American Birds which had been prepared according to the aforesaid Code of Rules, and *classified* in accordance with the views of the majority of the committee appointed by the Union to prepare it. In so far as the orders and families of this classification were concerned, the arrangement could be appreciated at a glance by reference to the Table of Contents of the book, and, as for the List itself, it not only was intended to represent the nomenclature of the Birds, but " a classification as well " (p. 15). At the close of the volume was presented a " Hypothetical List " to which had been referred those species and subspecies the zoological status of which could not be satisfactorily determined ; and following this was a list of the fossil species of North American birds.

As the years passed by a second edition of this book was